MULTILACUNAR NODAL ANATOMY IN MYTILARIA
(HAMAMELIDACEAE)[1]

A. Linn Bogle[2]

Multilacunar nodal anatomy associated with unique sheathing stipules in the genus *Mytilaria* (subfam. Exbucklandioideae) is reported for the first time in the Hamamelidaceae, a family usually characterized by trilacunar nodes. The number of gaps and traces ranged from eight to 12 in the nodes analyzed.

The significance of anatomical data from the stem-node-leaf continuum for systematic and phylogenetic studies is now generally recognized. The literature and the development of ideas in this field have been well reviewed by Howard (1979) and others (Carlquist, 1961; Radford *et al.*, 1974; Takhtajan, 1980). One of the major results of early studies of nodal anatomy in dicotyledons (Sinnott, 1914; Sinnott & Bailey, 1914) was the recognition of three major nodal types: trilacunar three-trace, unilacunar one-trace, and multilacunar multitrace. It was also established that the presence of stipules was usually correlated with trilacunar nodes, the absence of stipules with unilacunar nodes, and the presence of sheathing leaf bases or stipular structures with multilacunar nodes.

The purpose of this paper is to report the nodal structure of the unusual unistipulate leaves of the monotypic genus *Mytilaria* Lecomte. The nodes display a vascular pattern not previously known in the Hamamelidaceae but of apparent taxonomic significance.

In the Hamamelidaceae all of the approximately 30 currently recognized genera are stipulate. In most cases the stipules are paired, small, membranous, and ephemeral. However, the stipules of the three genera usually grouped in subfam. Exbucklandioideae are among the most unusual in the family. Those of *Exbucklandia* R. W. Brown and *Chunia* H. T. Chang are large, leathery, oblong to orbicular, and connate in the bud, completely enclosing the younger leaves and the shoot apex (Griffith, 1836; Lubbock, 1899; Chang, 1948). Their broadly attached bases leave a girdling scar at the node, imposing a jointed appearance on the stem. In contrast, the leaves of *Mytilaria laosensis* Lecomte are unique in the family in having a single, long, narrowly conical, sheathing stipule, which Lecomte (1924) thought consisted of two stipules united into a conical sheath. It attaches all the way around the stem, opens by a single
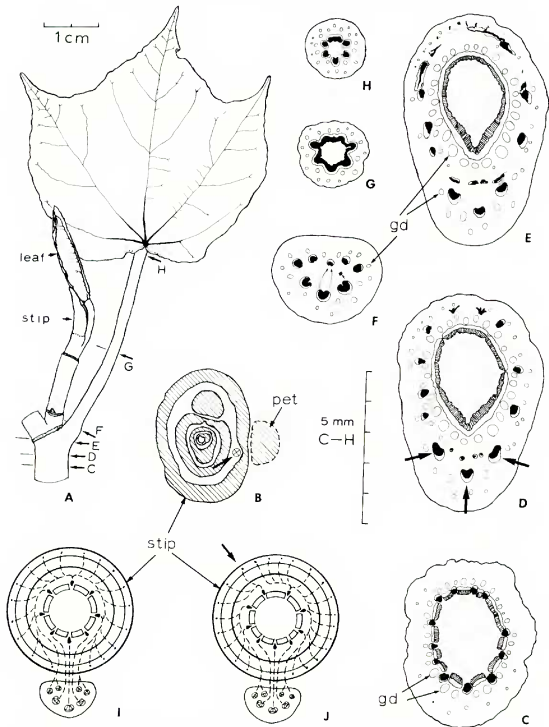
Nodal anatomy of *Mytilaria laosensis*: A, stem tip, showing young leaf prior to un-folding, with stipule still attached, and slightly older, expanding leaf with stipule scar at base (arrows indicate positions of sections in C–H); B, diagram of transverse section through bud, showing succession of 4 petiole–stipule sheath complexes in different stages of development (arrow indicates axillary bud; C, transverse section of internode, showing differentiation of 12 leaf traces (blank circles = gum ducts of ground tissue in C–H); D, transverse section of lower nodal area, showing 12 leaf traces in ground tissue, those farthest from leaf base beginning to branch (arrows indicate traces forming the 3 main abaxial bundles of petiole; remaining laterals contributing to petiole and/or stipule sheath); E, transverse section of upper nodal area, showing leaf base, part of stipule scar on side opposite leaf base, and horizontal course of some leaf traces on side of stem opposite

longitudinal suture that faces the petiole of the associated leaf, and at maturity is circumscissile caducous, also leaving the stem with a girdling scar and a jointed appearance (see Figure, A, B).

In general, anatomical data on the stem-node-leaf continuum in the Hamamelidaceae are fragmentary and scattered in a number of publications. Some of these studies (Sinnott, 1914; Sinnott & Bailey, 1914; Skvortsova, 1960; Bisht *et al.,* 1983) have emphasized the number of gaps in the stem stele and the number of traces departing from them to enter the leaf base. Others (Thouvenin, 1890; Morvillez, 1919; Tong, 1930; Chang, 1948; Covin, 1959; Skvortsova, 1960; Harjal *et al.,* 1984) have emphasized the number of vascular strands entering the leaf base (without reference to the structure of the node), the pattern formed by the vascular tissue at different levels in the petiole and midrib, and whether the vascular bundles are collateral or concentric in form. With regard to the subfamily Exbucklandioideae, several of these authors (Morvillez, 1919; Tong, 1930; Skvortsova, 1960) have included observations on the vascular structure of the petiole and midvein of one or another of the three genera of the subfamily in the context of broader studies of petiolar anatomy, but not on their nodal anatomy.

Among authors considering the anatomy of the node in the Hamamelidaceae, Sinnott (1914) described the Hamamelidaceae as being typically trilacunar. Sinnott and Bailey (1914, *pl. 44, fig. 4*) studied at length the origin of the vascular supply to the stipules, including those of *Hamamelis* L., which they designated (p. 453) as the "typical trilacunar dicotyledon," and indicated that in trilacunar nodes the stipular supply is typically derived from the lateral traces.

Skvortsova (1960, p. 126), as part of a broader study of petiole structure in the Hamamelidaceae and the Altingiaceae, investigated the nodal structure of leaves in which the vasculature "in the lower part of the petiole was established as an arc or semicircle" and concluded that a correlation existed between trilacunar nodal structure, three traces entering the leaf base, and a vascular pattern in the form of an arc or semicircle in the lower part of the petiole.

Bisht and colleagues (1983), on the other hand, reported unilacunar nodal structure for four genera of Hamamelidaceae (*Corylopsis* Sieb. & Zucc., *Distylium* Sieb. & Zucc., *Hamamelis, Parrotia* C. Meyer).

Among the authors who have concentrated on the vascular pattern of the petiole, Morvillez (1919, *fig. 5*) described three traces entering the leaf base in species of *Hamamelis, Parrotia, Fothergilla* L., and *Liquidambar* L. and implied a similar condition in *Disanthus* Maxim., *Exbucklandia* (as *Bucklandia*

---

leaf base; F, transverse section through base of petiole, showing vascular cylinder of 8 bundles; G, transverse section at mid-level of petiole, bundles forming vascular cylinder; H, transverse section through top of petiole, vascular cylinder broken up into discrete bundles, each of which will form leaf vein; I, diagrammatic representation of vascular pattern in node with 8 gaps and traces (dashed lines indicate branching patterns of lateral traces supplying petiole and stipule sheath in I, J); J, diagrammatic representation of vascular pattern in node with 9 gaps and traces. (Abbreviations: gd = gum duct, pet = petiole, stip = stipule.)

R. Br.), and *Altingia* Noronha. He described the structure of the vascular system at different levels in the petiole and the derivation of the major leaf veins from the petiole vasculature.

Tong (1930) described the vascular condition in the lower and upper parts of the petiole and the base, middle, and tip of the midvein for 20 species of 14 genera of Hamamelidaceae, including *Exbucklandia* (as *Bucklandia*). He described three collateral bundles in the lower part of the petiole for 17 of the species, one collateral bundle in two species of *Fothergilla*, and one concentric bundle in the lower part of the petiole of *Exbucklandia*, this giving rise to three concentric and five collateral bundles in the upper part of the petiole.

Covin (1959, *fig. 6*) illustrated the petiole vasculature of *Mytilaria* as being "polystelic" at mid-petiole level, while at the base of the midvein it formed a "simple fold" in *Mytilaria* and a "simple arc" in *Exbucklandia* (as *Bucklandia*).

Skvortsova (1960) examined the petiolar vascular system at the low, middle, and high levels in 22 genera of the family, including *Exbucklandia* and *Mytilaria*, and emphasized the configuration of the vasculature at mid-level. She found that all genera except *Liquidambar, Altingia, Mytilaria,* and *Embolanthera* Merr. have a cylinder of vasculature at mid-level. *Mytilaria* is illustrated (*fig. 1-22*) as having four arcuate bundles and an adaxial vascular band at mid-level, in contrast to a complete vascular cylinder at that level in *Exbucklandia* (*fig. 1-16*).

Chang (1948, p. 67), in his description of the new genus *Chunia*, provided the only direct comparative data for all three genera of Exbucklandioideae, stating that in the petiole of *Chunia* the vascular tissue "unites into a cylinder with prominent ridges," while in *Exbucklandia* (as *Bucklandia*) it is "horseshoe shaped," and in *Mytilaria* it is "arranged in discrete bundles."

MATERIALS AND METHODS

The observations reported here are based on hand sections, clearings, and serial sections of young, alcohol-preserved nodes and buds of *Mytilaria laosensis* obtained from the Biological Laboratory-Factory, Zhaoqing Training College, Zhaoqing, Guangdong, People's Republic of China (no collection number or data provided); on herbarium specimens of *Chunia* (*Wang 36075*, NYBG); and on personal field collections of *Exbucklandia populnea* (Bogle *1379, 1387*). All voucher materials are on deposit in the Botany and Plant Pathology Department of the University of New Hampshire (NHA).

For clearing, young nodes were bleached in 5% NaOH, washed in tap water, and cleared in 5% chloral hydrate. Transverse sections of nodes and petioles were made by standard paraffin-embedding techniques and stained with safranin–fast green (Sass, 1958). Hand sections were stained with phloroglucinol–50% HCl and mounted in glycerine.

OBSERVATIONS

Transverse sections of a young bud of *Mytilaria laosensis* revealed a condensed series of concentric stipular sheaths with their associated petioles. A

single suture was seen as a thin area in the stipule sheath opposite the petiole. There was no evidence of a second suture on the opposite side of the sheath to support an interpretation of two stipules united into a conical sheath. The stipule sheath encloses the related axillary bud (see FIGURE, B, arrow).

In sections of the stem of *Mytilaria* taken below the node of a young leaf, a number of leaf traces and gaps were clearly differentiated (see FIGURE, C). The gaps were more or less equally spaced around the circumference of the vascular cylinder. The number of gaps and traces ranged from eight to 12 in the nodes examined (see FIGURE, C, I, J).

The three traces originating nearest the leaf base moved directly and independently into the leaf base to form the three major abaxial bundles of the petiole vascular system. The five to nine bundles originating farther around the stem from the leaf base bent toward the leaf and ran more or less horizontally around the stem in the ground tissue, toward the leaf base, often anastomosing with adjacent traces to form an incomplete vascular ring around the node. As many as 18 to 24 minor branches diverge from the horizontal traces to provide the vascular supply to the base of the sheathing stipule (see FIGURE, I, J).

The trace farthest from the leaf base bifurcates after leaving the gap, sending branches in each direction around the node, as well as to the stipule (see FIGURE, D, I, J). Occasionally a leaf trace provided traces to the stipule but not to the leaf base (see FIGURE, J, arrow).

In the base of the petiole, seven or eight major bundles were observed, sometimes accompanied by minor cortical strands (see FIGURE, F). The three large abaxial bundles were each derived from single leaf traces originating from the three gaps directly opposite the leaf base, as described above. The two larger bundles in each angle of the petiole cross section resulted from the branching of a single bundle derived on each side of the node from fusion of the horizontal trace system (see FIGURE, I, J). Additional, smaller bundles may appear on the adaxial side of the petiole vascular cylinder, or in the central ground tissue, as derivatives of minor branches of the major bundles (see FIGURE, F, arrows).

At mid-petiole level the major bundles of the petiole base had fused into a fluted vascular cylinder (see FIGURE, G), which continued almost to the tip of the petiole. Just prior to joining the blade, the vascular cylinder again broke up into distinct bundles, each of which formed one of the major veins of the palmately veined leaf (see FIGURE, H).

In contrast to the multilacunar nodal structure of *Mytilaria*, the nodes in my material of *Exbucklandia* exhibit trilacunar, three-trace structure, with vascular supply to the large stipules derived from the lateral traces.

DISCUSSION

Nodal anatomy is generally considered to be a conservative feature of plant structure and to be a useful character at various levels in phylogenetic and taxonomic studies. However, Carlquist (1961, p. 87) warned that nodal anatomy can vary within a single plant, and that "there is no single point along

the petiole that could be called 'characteristic' or 'typical,' or be used to the exclusion of other sections for comparative purposes."

With regard to the Hamamelidaceae, Sinnott (1914) listed the family as trilacunar, while Skvortsova (1960) reported trilacunar nodes in those taxa of the family in which the vascular pattern in the lower part of the petiole is arc shaped or semicircular. Unfortunately, Skvortsova did not comment on the nodal structure of those taxa having a different vascular pattern in the lower petiole, and neither author was able to study all genera of the family. My observations (unpublished) on the nodes of foliage leaves of various genera of Hamamelidaceae (*Altingia, Liquidambar, Rhodoleia* Champ., *Exbucklandia, Disanthus, Hamamelis, Eustigma* Gardner & Champ., *Corylopsis* Sieb. & Zucc., *Sinowilsonia* Hemsley, *Parrotia, Parrotiopsis* Schneider, *Distylium, Matudaea* Lundell) indicate that all have trilacunar, three-trace nodes.

There are, however, reports in the literature that present conflicting information. Bisht and colleagues (1983, *fig. 1*) reported unilacunar, one-trace nodes in *Distylium racemosum* Sieb. & Zucc., *Hamamelis japonica* Sieb. & Zucc., and *Hamamelis virginiana* L. (which Sinnott & Bailey, 1914, regarded as the typical trilacunar dicotyledon); unilacunar, three-trace nodes in *Parrotia persica* C. Meyer, and unilacunar, four-trace nodes in *Corylopsis spicata* Sieb. & Zucc. In contrast, Harjal and co-workers (1984, *table 2*), considering only the petiole vasculature, reported only one strand entering the petiole in *Corylopsis spicata, Distylium racemosum, Rhodoleia forrestii* Chun ex Exell, and *Trichocladus crinitis* Pers., as opposed to three in *Liquidambar styraciflua* L. and *Parrotiopsis jacquemontiana* Rehder. Thouvenin (1890), also considering only the petiole vasculature, reported three bundles departing from the stem (without reference to the number of lacunae) and entering the petiole in both *Trichocladus crinitis* and *T. elliptica* Ecklon & Zeyher.

Thus, several taxa (*Distylium racemosum, Hamamelis japonica, H. virginiana, Corylopsis spicata, Parrotia persica*) have been reported or observed to have either trilacunar, three-trace nodes, or unilacunar nodes with one, three, or four traces. These and other inconsistencies suggest the need for a more thorough and detailed study of the stem-node-leaf continuum in the Hamamelidaceae, particularly with regard to intraspecific variation.

Anatomical characters from the stem-node-leaf continuum have been used in some taxonomic studies regarding the relationships of genera and subfamilies in the Hamamelidaceae, including *Mytilaria* and *Exbucklandia.* Morvillez (1919) considered the similar petiolar structure in *Disanthus* (which now comprises subfam. Disanthoideae) and *Exbucklandia* (as *Bucklandia,* the two genera together then constituting tribe Bucklandieae) to be intermediate forms, linking the tribe Balsamiflueae (*Liquidambar* and *Altingia,* now subfam. Liquidambaroideae) to the remainder of the Hamamelidaceae. Skvortsova (1960), on the other hand, considered the data from petiole vascular structure to support the segregation of *Liquidambar* and *Altingia* as a family (Altingiaceae), to which she suggested that *Mytilaria* is related.

The distinctive vegetative morphology shared by *Exbucklandia, Chunia,* and *Mytilaria* makes them easily identifiable as the only members of subfam. Exbucklandioideae. However, the three genera differ significantly in floral morphology, and in recent years they have been separated by some authors into

two subfamilies. Chang (1973) segregated *Mytilaria* and *Chunia* in the new (and sixth) subfamily Mytilarioideae, leaving only *Exbucklandia* in the Exbucklandioideae. Huang and Lee (1982) supported this segregation on the basis of wood anatomy, suggesting a closer relationship of the Mytilarioideae to subfam. Disanthoideae than to any of the other subfamilies (i.e., Liquidambaroideae, Rhodoleioideae, Hamamelidoideae). Takhtajan (1980), on the other hand, listed subfam. Chunioideae (rather than Mytilarioideae) as one of six subfamilies in the Hamamelidaceae but did not indicate which of the three genera of Exbucklandioideae he would assign to it or his reasons for removing them from the Exbucklandioideae.

Mytilaria is clearly set apart from the other two genera of Exbucklandioideae by its single, conical, sheathing stipules; its gum ducts (secretory canals) in the ground tissue throughout the plant, including the flowers; its numerous, complete flowers with nearly inferior ovaries sunken in a long, fleshy spike; its petals and stamen filaments fused basally into a short tube; and its ten stamens with horned filaments surmounted by hooded anthers, connivent in a cycle over minute styles and stigmas. The presence of multilacunar nodes in *Mytilaria,* as opposed to trilacunar nodes and paired stipules in *Exbucklandia,* adds yet another distinctive character to this list, suggesting that separation of *Mytilaria* from *Exbucklandia* is more appropriate at the tribal level within subfam. Exbucklandioideae than as the separate subfam. Mytilarioideae.

The position of *Chunia* in such a subdivision of the Exbucklandioideae is as yet uncertain. Its floral morphology is distinctive (naked, bisexual flowers sunken in a relatively-few-flowered, short spike) and is perhaps closer to that of *Exbucklandia* than that of *Mytilaria.* It also shares paired, connate stipules with *Exbucklandia.* However, my preliminary observations on the few nodes available for study indicate that it, too, has multilacunar nodes. This would tend to emphasize the unity of the three genera as a single subfamily. At the same time, it could be taken as support for the taxonomic separation of *Mytilaria* and *Chunia* from *Exbucklandia,*as proposed by Chang (1973). However, the significant differences in floral morphology between *Mytilaria* and *Chunia* may militate against their being paired in this way. Investigation is continuing on *Chunia.*

ACKNOWLEDGMENTS

LITERATURE CITED

BISHT, P. S., C. B. MALASI, & G. S. PALIWAL. 1983. Nodal organization in Hamamelididae. Geophytology **13:** 88–92.

CARLQUIST, S. 1961. Comparative plant anatomy. Holt, Rinehart and Winston, New York.

CHANG, H. T. 1948. Additions to the hamamelidaceous flora of China. Sunyatsenia 7: 63–74.

———. 1973. A revision of the hamamelidaceous flora of China. Sunyatsen Univ. Bull. 1: 54–71.

COVIN, J. 1959. L'appareil libéro-ligneux foliaire des Hamamelidacées. Bull. Soc. Bot. N. France 12: 31–33.

GRIFFITH, W. 1836. Description of two genera of the family of Hamamelideae, two species of *Podostemon* and one species of *Kaulfussia*. Asiat. Res. 19: 94–114. *pls. 13–18.*

HARJAL, N., P. S. BISHT, & G. S. PALIWAL. 1984. Foliar vasculature as an aid to the classification of Hamamelididae. Pp. 282–300 *in* G. S. PALIWAL, ed., The vegetational wealth of the Himalayas. Puja Publishers, Delhi.

HOWARD, R. A. 1979. The stem-node-leaf continuum of the Dicotyledoneae. Pp. 76–87 *in* C. R. METCALFE & L. CHALK, Anatomy of the dicotyledons. ed. 2. Vol. 1.

HUANG, G., & C. LEE. 1982. Anatomical studies of *Chunia* wood. [In Chinese with English abstract.] Acta Bot. Sinica 24: 506–511.

LECOMTE, H. 1924. Une Hamamélidacée nouvelle d'Indochine. Bull. Mus. Hist. Nat. (Paris) 30: 503–507.

LUBBOCK, J. 1899. On buds and stipules. Kegan Paul, Trench, Truebner & Co., Ltd., London.

MORVILLEZ, M. F. 1919. L'appareil conducteur foliaire des Hamamélidacées et des formes voisines. Compt. Rend. Hebd. Séances Acad. Sci. 169: 542–545.

RADFORD, A. E., W. C. DICKISON, J. R. MASSEY, & C. R. BELL. 1974. Vascular plant systematics. Harper and Row, New York.

SASS, J. E. 1958. Botanical microtechnique. ed. 3. Iowa State University Press, Ames.

SINNOTT, E. W. 1914. Investigations on the phylogeny of the angiosperms. I. The anatomy of the node as an aid in the classification of angiosperms. Amer. J. Bot. 1: 303–322, *pls. 30–35.*

——— & I. W. BAILEY. 1914. Investigations on the phylogeny of the angiosperms. 3. Nodal anatomy and the morphology of stipules. Amer. J. Bot. 1: 441–453. *pl. 44.*

SKVORTSOVA, N. T. 1960. The anatomical structure of the conducting system of leaf petioles of representatives of families Hamamelidaceae and Altingiaceae. Dokl. Akad. Nauk SSSR 133: 1231–1234.

TAKHTAJAN, A. 1980. Outline of the classification of flowering plants (Magnoliophyta). Bot. Rev. (Lancaster) 46: 225–359.

THOUVENIN, M. 1890. Recherches sur la structure des Saxifragacées. Ann. Sci. Nat. Bot., ser. 7. 12: 1–174.

TONG, K. 1930. Studien ueber die Familie der Hamamelidaceae, mit besonderer Berücksichtigung der Systematik und Entwicklungsgeschichte von *Corylopsis*. Bull. Dept. Biol. Sun Yatsen Univ. 2.